Revista Brasileira de Entomologia xxx (2016) xxx–xxx

SOCIEDADE BRASILEIRA DE ENTOMOLOGIA
FUNDADA EM 1937

REVISTA BRASILEIRA DE
Entomologia
A Journal on Insect Diversity and Evolution
www.rbentomologia.com

Biology, Ecology and Diversity

Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae)

Camila Fediuk de Castro-Guedes[a,*], Lúcia Massutti de Almeida[a], Susete do Rocio Chiarello Penteado[b], Mauricio Osvaldo Moura[c]

[a] *Laboratório de Sistemática e Bioecologia de Coleoptera, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil*
[b] *Laboratório de Entomologia, Embrapa Florestas, Colombo, PR, Brazil*
[c] *Laboratório de Dinâmicas Ecológicas, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, PR, Brazil*

ARTICLE INFO

Article history:
Received 30 September 2015
Accepted 24 March 2016
Available online xxx
Associate Editor: Rodrigo Krüger

Keywords:
Aphids
Development time
Harlequin ladybird
Life table

ABSTRACT

The biology, reproductive variables and population growth indicators of *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) fed on three diets, namely *Cinara atlantica* (Wilson, 1919) (Hemiptera: Aphididae), *Brevicoryne brassicae* (Linnaeus, 1758) (Hemiptera: Aphididae), and frozen eggs of *Anagasta kuehniella* (Zeller, 1879) (Lepidoptera: Pyralidae), were evaluated. With all three diets, birth rate was higher than mortality, resulting in positive r_m values and thus indicating population growth. Under the conditions used in the experiments, *H. axyridis* was able to survive, develop and reproduce normally. This demonstrates that are different kind of food that can be essential for supporting the reproduction of some species of Coccinellidae, but not with the same optimization of preferred prey.

© 2016 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Introduction

Coccinellidae is a very heterogeneous group with respect to feeding behavior and the evolution of their food specificity includes transitions across kingdoms (Plantae, Animalia and Fungi) and trophic levels (herbivorous and primarily carnivorous) (Sutherland and Parrella, 2009). Food resources used by predatory coccinellids depend heavily on the abundance of prey available in the environment where they live (Dixon, 2000). This fact makes many of these predators polyphagous, i.e., they are able to feed on a variety of food, making it difficult to determine for some groups a correct relationship between predator and prey (Hodek, 1973). This behavior is often seen as an emergency strategy when the preferred food is scarce. Polyphagous species can have great importance in the use of integrated pest control, because they can be more easily mass-produced with artificial diets, or even their numbers increase considerably in the field with alternative food sources (Hodek and Honěk, 1996; Guedes, 2013).

The amount and the quality of food is very important because influences directly on the biological aspects of Coccinellidae (Dixon, 2000). When the ingested food is few or of poor quality, the development time usually increases and the reproductives rates, i.e. oviposition, fecundity and fertility decrease (Hodek et al., 2012). Given the relevance of coccinellids for biological control, much attention has been given to documenting feeding habits within the family (Giorgi et al., 2009).

Food that provides complete development and reproduction of coccinellids is considered essential, such as aphis, psyllids and mealybugs for predators, while that which serves only as an energy source and is able to prolong survival is characterized as alternative (Hodek, 1996). Some studies show that species of Coccinellidae are able to reproduce feeding on non-aphid prey, thus demonstrating the importance of these food (Hodek et al., 1978; Lundgren and Wiedenmann, 2004; Omkar, 2003; Berkvens et al., 2008; Lundgren, 2009).

Alternative food are important components in most diets of coccinellids, because they are an essential part in the life history of several species. Nectar, honeydew, pollen, fruits, vegetation and fungi are routinely consumed by coccinellids under laboratory conditions (Lundgren, 2009).

Among the predatory Coccinellidae, *Harmonia axyridis* (Pallas, 1773) is used in the biological control of aphids considered pests of many crops of economic importance (Koch, 2003), especially because of its high capacity to locate populations of aphids in space and time (Osawa, 2000). However, this species is also well known for its polyphagia. *Harmonia axyridis* is capable of consuming over 77 different prey species, found in approximately 85 plant species in 35 families. Their prey include aphids, coccids, psyllids, and they

* Corresponding author.
E-mail: camifc@yahoo.com (C.F. de Castro-Guedes).

http://dx.doi.org/10.1016/j.rbe.2016.03.003
0085-5626/© 2016 Sociedade Brasileira de Entomologia. Published by Elsevier Editora Ltda. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

even consume pollen and fruits (Koch, 2003; Koch et al., 2006; Martins et al., 2009; Castro et al., 2011; Guedes, 2013; Guedes and Almeida, 2013).

Most studies assessing the feeding of *H. axyridis* are based on laboratory experiments and field observations of a few individuals. This makes it difficult to establish whether the consumption of certain food is a common occurrence (Maurice et al., 2011). It is very important to determine the relationship of this species to its food resources especially because it is an introduced and also an extremely polyphagous species. Thus, this study aimed to analyze the biology, reproductive variables and population growth indicators of *H. axyridis*, fed three different diets.

Material and methods

Frozen eggs of *Anagasta kuehniella* (Zeller, 1879) (Lepidoptera: Pyralidae) is one of the most known and used due to its success in mass rearing of several species, including several coccinellids predators. Therefore and because of the easy access to this food, it was chosen as one of the diets tested. In Brazil, *H. axyridis* is able to feed on two species of aphids commonly found and already reported as pests (Castro et al., 2011). *Cinara atlantica* (Wilson, 1919) (Hemiptera: Aphididae), the giant conifer aphid-of-pine, was detected in Brazil in 1998, attacking pine plantations (Pinaceae) *Pinus taeda* Linnaeus and *Pinus elliottii* Engelm (Iede et al., 1998; Lazzari & Zonta-de-Carvalho, 2000). *Brevycorine brassicae* Linnaeus, 1758 is one of the most harmful pests and more consistently present in cabbage crops (Theunissen 1989).

Stock populations

Cinara atlantica (Wilson, 1919) (Hemiptera: Aphididae)

Aphids were collected in the field, on branches of *Pinus taeda* Linnaeus and *Pinus elliottii* Engelm infested with *Cinara atlantica*, in Curitiba, PR and taken to the insect rearing laboratory, Zoology Department, Universidade Federal do Paraná. They were kept at $21 \pm 1\,^{\circ}C$, $70 \pm 10\%$ relative humidity and 24-hour photoperiod to keep a sufficient supply for performing the bioassays.

Aphids were taken from pine branches from the field, with the help of a fine brush and transferred to the new seedlings purchased at a commercial nursery. The seedlings were replaced when required to maintain the stock population, later used to feed the coccinellids, using the same transfer technique. Aphids were separated by size: small (1st and 2nd instar nymphs), medium (3rd and 4th instar nymphs) and adult aphids.

Brevicoryne brassicae Linnaeus, 1758 (Hemiptera: Aphihidae)

Aphids were collected with the aid of a fine brush in cabbage crops (*Brassica oleracea* Linnaeus), variety of the Acephala group in Campo Magro, PR and transferred to seedlings planted at the Universidade Federal do Paraná, Curitiba, PR.

The infestation of aphids and replacement of cabbage leaves were performed when necessary to maintain a supply for later use of the population of aphids to feed *H. axyridis*, using the same transfer technique and separated by size as above.

Anagasta kuehniella (Zeller, 1879) (Lepidoptera: Pyralidae)

Frozen *A. kuehniella* eggs were obtained from a rearing company and kept in a freezer at $-20\,^{\circ}C$ in laboratory. The eggs were removed from the freezer and given to the coccinellids after thawing for five minutes on 9-cm diameter filter paper slightly moistened.

Harmonia axyridis

For creating the stock, *H. axyridis* adults were collected on pine branches in October 2011 in Curitiba, Brazil and raised in plastic containers of 500 ml in brood chambers $25 \pm 1\,^{\circ}C$, $70 \pm 10\%$ RH and 12:12 h L:D. The adults were sexed according to the method of McCornack et al. (2007) and kept in pairs for obtaining eggs, which were later transferred to Petri dishes with moist filter paper. After hatching, the larvae were individually placed in Petri dishes lined with filter paper and a cotton swab moistened with a drop of honey. To maintain the stock population, three diets were given simultaneously (so as not to induce preference for the type of food in the daily experiments) ad libitum and once daily. From the formation of prepupae until the emergence of adults, insects were kept under the same conditions described above, with no food. Third generation individuals were used for the bioassays.

Determination of body weight

The 1st and 2nd instar larvae and the newly emerged adults were weighed about 1 h after hatching and emergence, while the 3rd and 4th instar larvae of were weighed upon emergence.

Experimental design

The following diets were tested on *H. axyridis*: Diet 1: *Cinara atlantica*; Diet 2: *Brevicoryne brassicae*; and Diet 3: *Anagasta kuehniella*. There were 15 replicates for each diet.

After egg hatching, the larvae were individually placed in Petri dishes lined with filter paper and a cotton swab moistened with a drop of honey to begin the experiments. The food was offered *ad libitum* and replaced daily. Small aphids were offered for the 1st instar larvae, medium-size and adult aphids for the other instars. After adult emergence, they were sexed and maintained in couples until the conclusion of the experiments. Oviposition and egg hatching of each female were counted and recorded in spreadsheets to calculate fecundity, fertility and specific fertility. The complete cycle of each individual was followed to construct life and fertility tables. The exchange and cleaning of the containers were done every 48 h and the observations were made daily.

Statistical analysis

All statistical analyses were performed in R 2.1.2 environment (R Development Core Team, 2011). To analyze the existence of differences between the diets in relation to development period, body weight and reproductive variables of *H. axyridis*, the data were fitted using a generalized linear model (GLM) and an error distribution of the inverse Gaussian family. Tukey's contrasts ($p \leq 0.05$) were used for back-comparisons a posteriori.

The analysis for the development period was conducted for the egg, four larval instars, prepupa and pupa. Body weight data was analyzed for the four larval instars and the newly emerged adults. The analysis for reproductive variables reproductive parameters (pre-oviposition, oviposition and post-oviposition, fecundity, fertility, eggs/day, posture, eggs/mass) was performed for females, and longevity was analyzed for adults. For all these analyses, diet was used as a predictor variable.

For GLM, we was used the MASS library (Venables and Ripley, 2002) and effects (Fox, 2003) and the multcomp library was used for subsequent analysis (Hothorn et al., 2008).

The life tables and fertility and population growth indicators were constructed taking into account the performance of individuals with three diets and prepared by the computational system TabVida (Penteado et al., 2010). The reproductive indicators were determined as follows: specific fertility (mx: number of females

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

Table 1
Development period in days (mean ± standard deviation) of *Harmonia axyridis* (Pallas, 1773) fed with three different diets: *Cinara atlantica* (Wilson, 1919); *Brevicoryne brassicae* Linnaeus, 1758; and frozen eggs of *Anagasta kuehniella* (Zeller, 1879), at 25 °C 12:12 h L:D and 70% ± 10% RH.

Development period	Diets		
	C. atlantica	*B. brassicae*	*A. kuehniella*
Egg	3.27 ± 0.46 ab	3.00 ± 0.00 a	3.33 ± 0.49 b
1° instar	3.47 ± 0.52 a	2.80 ± 0.86 b	2.80 ± 0.41 b
2° instar	2.60 ± 0.63 a	2.87 ± 0.83 a	2.80 ± 0.94 a
3° instar	2.67 ± 0.49 a	3.2 ± 0.83 a	2.73 ± 0.70 a
4° instar	4.47 ± 0.52 a	4.6 ± 0.63 a	5.00 ± 0.84 a
Prepupa	1.00 ± 0.00 a	1.00 ± 0.00 a	1.00 ± 0.00 a
Pupa	4.87 ± 0.35 a	5.00 ± 0.92 a	5.13 ± 0.83 a
Total	22.35	22.47	22.79

* Means values within a line followed by the same small letter are not significantly different, $p < 0.05$, Tukey's test.

produced/female); net reproductive rate (R_o: $\sum$(mxlx)); interval between generations (T: $\sum$ (mxlx.x/$\sum$ (mxlx))); intrinsic rate of increase (r_m: In R_o/T); finite rate of population increase (λ: e^{r_m}) and population doubling time (DT: In(2)/r_m).

Parameters of fertility life table and their standard errors were estimated using the Jackknife method (Meyer et al., 1986) and the averages compared by "*t*" unilateral.

Results

Development period

The mean incubation period was statistically significant differences between diets 2 and 3 (Deviance = 0.093; Df = 2; $p = 0.03$) (I1). There was a statistical difference in the development period between the three diets only in the 1st instar, that was longer when *H. axyridis* was fed with diet 1 (*C. atlantica*) (Deviance = 0.466; Df = 2; $p = 0.006$). When individuals were fed *C. atlantica*, the mean length of the 1st, 2nd, 3rd and 4th instars was respectively 3.47, 2.60, 2.67 and 4.47 days. The prepupa period lasted on average 1 day, while the pupa stage was 4.87 days, and the total development period from egg to adult emergence was 22.35 days (Table 1).

In individuals receiving diet 2, *B. brassicae*, the mean length of the 1st, 2nd, 3rd and 4th instar was respectively 2.80, 2.87, 3.20 and 4.60 days. The prepupa period lasted on average one day, while the pupa period five days, and the total development period was 22.47 days (Table 1).

In individuals fed with frozen eggs of *A. kuehniella*, the mean length of the 1st, 2nd, 3rd and 4th instar was respectively 2.80, 2.80, 2.73 and 5.00 days. The prepupa stage lasted on average one day, while the pupa one 5.13 days, and the total development period was 22.79 days (Table 1).

Table 3
Reproductive period and longevity (days) (mean ± standard deviation) of *Harmonia axyridis* (Pallas, 1773) fed with three different diets: *Cinara atlantica* (Wilson, 1919); *Brevicoryne brassicae* Linnaeus, 1758; and frozen eggs of *Anagasta kuehniella* (Zeller, 1879), at 25 °C 12:12 h L:D and 70% ± 10% RH.

Variables	Diets		
	C. atlanticak	*B. brassicae*	*A. kuehniella*
Longevity	95.47 ± 9.72 a	92.40 ± 2.38 a	91.13 ± 25.53 a
Pre-oviposition	6.93 ± 1.22 a	6.13 ± 0.35 a	7.20 ± 0.82 a
Oviposition	80.47 ± 10.36 a	78.73 ± 2.49 a	77.20 ± 26.19 a
Post-oviposition	8.07 ± 0.88 a	7.33 ± 0.72 ab	6.73 ± 0.91 b

* Means values within a line followed by the same small letter are not significantly different.

Table 4
Fecundity and fertility; eggs per day; egg mass and egg per egg mass (mean ± standard deviation) of *Harmonia axyridis* (Pallas, 1773) fed with three different diets: *Cinara atlantica* (Wilson, 1919); *Brevicoryne brassicae* Linnaeus, 1758; and frozen eggs of *Anagasta kuehniella* (Zeller, 1879), at 25 °C 12:12 h L:D and 70% ± 10% RH.

Variables	Diets		
	C. atlantica	*B. brassicae*	*A. kuehniella*
Fecundity	747.53 ± 71.75 a	641.00 ± 59.36 b	555.50 ± 74.56 c
Fertility	671.07 ± 87.26 a	475.07 ± 77.54 b	313.80 ± 86.37 c
Eggs/day	9.33 ± 0.40 a	8.14 ± 0.52 ab	7.58 ± 2.14 b
N° of egg masses	32.87 ± 8.22 a	27.07 ± 3.37 ab	24.47 ± 7.22 b
Eggs/egg masses	24.08 ± 6.30 a	23.78 ± 1.13 a	23.71 ± 4.55 a

* Means values within a line followed by the same small letter are not significantly different.

Body weight

Statistically, diet 2 and 3 were similar, except the newly emerged adult where diet 1 and 2 were more similar (Table 2).

Longevity and reproductive capacity

Adult longevity (Deviance = 0.016; Df = 2; $p = 0.747$), pre-oviposition (Deviance = 0.011; Df = 2; $p = 0.696$), and oviposition (Deviance = 0.012; Df = 2; $p = 0.855$) period were similar with the three diets, with no statistical difference (Table 3).

The fecundity was significantly different for the three diets, with diet 1 showing the highest number of 747.53 eggs, compared to diets 2 (641 eggs) and 3 (555.5 eggs). The mean daily number of eggs produced per female was statistically different with diets 1 (9.33) and 3 (7.58) (Deviance = 0.271; Df = 2; $p = 0.005$). The fertility of *H. axyridis* eggs was significantly different for the three diets used, where it was highest with diet 1, i.e., 671.07 (Deviance = 4.245; Df = 2; $p = <2.2e^{-16}$) (Table 4).

The mean number of egg masses per female of *H. axyridis* was significantly different for the diets 1 and 3 (32.87 and 24.47 oviposition, respectively) (Deviance = 0.683; Df = 2; $p = 0.002$). There was no significant difference in number of eggs per egg mass for the three diets (Deviance = 0.002; Df = 2; $p = 0.972$). (Table 4) and the

Table 2
Body mass in miligrams (mean ± standard deviation) of Harmonia axyridis (Pallas, 1773) fed with three different diets: *Cinara atlantica* (Wilson, 1919); *Brevicoryne brassicae* Linnaeus, 1758; and frozen eggs of *Anagasta kuehniella* (Zeller, 1879), at 25 °C 12:12 h L:D and 70% ± 10% RH.

Development period	Diets		
	C. atlantica	*B. brassicae*	*A. kuehniella*
1° instar	0.0018 ± 0.0007 a	0.0013 ± 0.0004 ab	0.0012 ± 0.0006 b
2° instar	0.0033 ± 0.0012 a	0.0023 ± 0.0004 b	0.0023 ± 0.0008 b
3° instar	0.0055 ± 0.0013 a	0.0045 ± 0.0005 b	0.0048 ± 0.0010 ab
4° instar	0.0079 ± 0.0007 a	0.0076 ± 0.0005 a	0.0074 ± 0.0006 a
Newly emerged adult	0.0258 ± 0.0010 a	0.0255 ± 0.0005 a	0.0247 ± 0.0002 b

* Means values within a line followed by the same small letter are not significantly different.

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

post-reproductive period (Deviance = 0.245; Df = 2; $p = 7.928e^{-05}$) for *H. axyridis* females was longest with diet 1, with significant difference compared with diet 3 (Table 3).

Life and fertility table

Specific fertility was highest with diet 1 (*C. atlantica*), followed by diets 2 (*B. brassicae*) and 3 (*A. kuehniella*) (Figs. 1–3). For this variable, it is noteworthy that the tool used for the calculation of indicators of population growth and analysis between treatments, TabVida (Penteado et al., 2010), recorded reproduction up to the 100th day. However, with diet 1 as well as diet 3, there was reproduction after the 100th day in 3 and 6 individuals, respectively (Figs. 1 and 3).

In diet 1, the oviposition period was from the 6th to 98th day, with the highest specific fertility observed in the age range between 32 and 64 days. The survival rate (lx) remained constant until the age of 79.5 days when a death was recorded, where a marked decrease was observed starting at 90.5 days of age (lx = 0.73) (Fig. 1).

With diet 2, the oviposition period was in the age range of 7 to 89 days, and the highest specific fertility observed between the 7th and 56th day. The survival rate (lx) remained constant up to 89.5 days, when a death was recorded, and there was a sharp decrease as of 92.5 days of age (lx = 0.53) (Fig. 2).

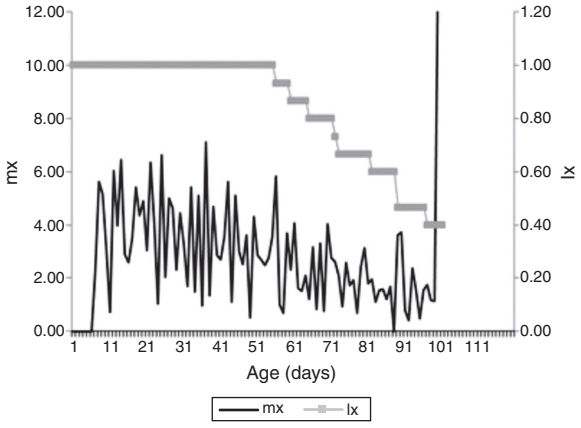

Fig. 1. Survival probability (lx), expressed in percentage, and specific fertility (mx) expressed as average number of eggs per day of *Harmonia axyridis* (Pallas, 1773) fed on *Cinara atlantica* (Wilson, 1919). Temperature 25 ± 1 °C, 70 ± 10% RU and humidity and 12:12 h L:D.

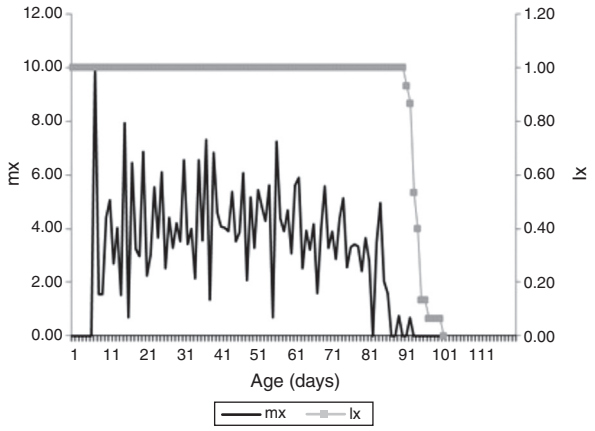

Fig. 2. Survival probability (lx), expressed in percentage, and specific fertility (mx) expressed as average number of eggs per day of *Harmonia axyridis* (Pallas, 1773) fed on *Brevicoryne brassicae* Linnaeus, 1758. Temperature 25 ± 1 °C, 70 ± 10% RU and humidity and 12:12 h L:D.

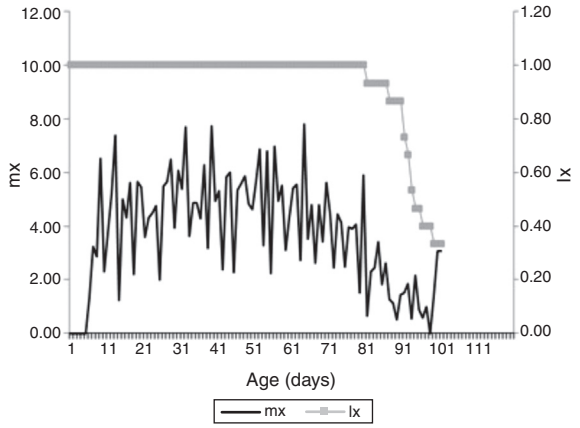

Fig. 3. Survival probability (lx), expressed in percentage, and specific fertility (mx) expressed as average number of eggs per day of *Harmonia axyridis* (Pallas, 1773) fed on *Anagasta kuehniella* (Zeller, 1879). Temperature 25 ± 1 °C, 70 ± 10% RU and humidity and 12:12 h L:D.

In diet 3, the oviposition period occurred between 7 and 100 days, with the highest specific fertility observed between 25 and 37 days. The survival rate (lx) remained constant up to the 54.5th day when a death was recorded, and there was a sharp decrease in survival as of the 81.5th day (lx = 0.60) (Fig. 3).

Estimated reproductives indicators of life and fertility table

The net reproduction rate (R_o) was higher with diet 1 (*C. atlantica*), 366.52, followed by diet 2, (*B. brassicae*), 320.41 and diet 3 (*A. kuehniella*), 249.21, where there was a highly significant difference between diets 1 and 3. In this study, there was no significant difference between the three diets for time interval between consecutive generations (*T*) (Table 5).

In the three diets studied, *H. axyridis* showed a higher birth rate than mortality rate, resulting in positive r_m values indicating population growth, with no statistical difference between the treatments. The finite rate of population increase (λ) and population doubling time (DT) values were similar for diets, with no significant difference between treatments (Table 5).

Table 5
Estimated reproductives indicators of life and fertility table (±SE) for *Harmonia axyridis* (Pallas, 1773) fed with three different diets: *Cinara atlantica* (Wilson, 1919); *Brevicoryne brassicae* Linnaeus, 1758; and frozen eggs of *Anagasta kuehniella* (Zeller, 1879), at 25 °C 12:12 h L:D and 70% ± 10% RH.

Reproductive indicators	Diets		
	C. atlantica	*B. brassicae*	*A. kuehniella*
Net reproductive rate (R_o)	373.77 a	320.5 a	277.43 b
Time interval between consecutive generations (*T*)	46.22 a	44.27 a	47.02 a
Intrinsic rate of increase (r_m)	0.13 a	0.13 a	0.12 a
Finite rate of population increase (λ)	11389 a	11388 a	11275 a
Population doubling time (DT)	5.33 a	5.33 a	5.78 a

* Values within a line followed by the same small letter are not significantly different.

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

Discussion

The temperature and type of food influence development, body weight, longevity and reproductive variables of various species of Coccinellidae (Blackman, 1965; De Clercq et al., 2005; Jalali et al., 2009; Castro et al., 2011). The results of this experiment suggest that *H. axyridis* is able to complete its development period and reproduction, feeding on the three diets offered.

The development period of *H. axyridis* was similar in length with the three diets provided. Under similar conditions, using *C. atlantica* as food, the results obtained by other authors were close to ours, such as Castro et al. (2011) and Santos et al. (2014).

According to Santos et al. (2009), the development period was shorter, but the experiments were performed at a higher temperature, 27 °C, which may explain the more rapid development. However, Specty et al. (2003) also obtained a more rapid development, with a lower temperature, 23.5 °C. These results indicated that in addition to temperature, another important factor is the condition of the food used. In both works, *A. kuehniella* eggs offered were fresh, while those in this study were frozen.

Several studies have indicated that the 1st instar larvae of coccinellids have difficulty feeding on large and very active prey (Majerus, 1994; Phoofolo and Obrycki, 1995; Dixon, 2000; Jalali et al., 2009). This may explain the longer duration of the 1st instar of H. axyridis, when fed with diet 1, *C. atlantica*, a very large aphid relative to the size of these larvae.

Another possible reason for the difference in development time would be that some aphid species appear to be immediately accepted as food by larvae and adults, while others require a slower recognition, which in this case would reduce the fitness of the individuals, causing a longer duration of the larval stages (Soares et al., 2005).

Studies have shown that differences in aphid species directly affect instar duration of coccinellids. Cinara atlantica aphids appear to have better nutritional value, due to their larger size, which can shorten instar duration, compared to other species (Pervez and Omkar, 2004). Maurice et al. (2011) evaluated the development period of *Coccinella transversalis* (Fabricius, 1781) fed with eight different aphid species and found that larval development was completed with all diets, but with differences in duration.

For body weight gain, besides they were similar, the closest relationship was between diets 2 and 3 showing again the influence of quantity and quality of food. A mixed diet seems to promote more robust individuals, as demonstrated by De Clercq et al. (2005), who obtained heavier adults of Adalia bipunctata, with a higher oviposition rate, when the larvae were fed a mixed diet if *A. kuehniella* eggs and pollen than when fed only Aphis pisum.

Adult longevity was similar in the three diets used. For individuals fed with *C. atlantica*, Castro et al. (2011) obtained a close longevity (89.13 days), whereas Santos et al. (2014), besides the same temperature, found a lower lone (85.6 days). Santos et al. (2009) observed a shorter longevity for *H. axyridis* adults fed *A. kuehniella* eggs, 74.1 days for females and 67.3 days for males, probably due to higher temperature used in the experiment (27 °C).

Harmonia axyridis adults fed a mixed diet consisting of *A. kuehniella* eggs, *Aphis fabae* Scopoli, 1763 and *Myzus persicae* Sulzer, 1766 had a lower longevity (Soares et al., 2001). Soares et al. (2005) showed that *H. axyridis* fed a diet consisting of a mixture of different species of aphids adapted better than with a single species of aphids. However, (Niijima et al., 1997) tested various diets in the laboratory, including those composed of two or more species of aphids, and noted that they were inefficient in relation to the development and reproduction of *H. axyridis* (Niijima et al., 1997).

The fact that reproductive capacity was satisfactory for the three diets used indicated that mass-rearing of H. axyridis can be performed using the three diets, but with diet 1, *C. atlantica*, the overall performance was better. The results obtained by Castro et al. (2011) and Santos et al. (2014), using the same diet, were similar to ours, demonstrating the excellent performance of *H. axyridis* when fed with this species of aphid.

With regard to diet 2, Ashaf (2010) tested three species of aphids as food for *C. septempunctata*: *B. brassicae*, *Macrosiphum roseae* (Linnaeus, 1758) and *Rhopalosiphum maidis* (Fitch, 1856) and noted that, besides that all three diets were suitable for the coccinellid, *B. brassicae* was less consumed and prevented oviposition, which was not observed in this experiment with *H. axyridis*.

According to Santos et al. (2009), individuals fed with *A. kuehniella* eggs showed a much shorter oviposition period than in the present study, but the authors did not evaluate other factors such as number of ovipositions and fertility, making it difficult to make a more detailed comparison of results.

Hamasaki and Matsui (2006) observed that larvae and adults of *Propylea japonica* fed frozen *A. kuehniella* eggs had a much lower reproductive capacity compared to larvae that were fed with *Aphis pisum* and adults with frozen *A. kuehniella* eggs, indicating the importance of the type of food both in the larval and adult stages. Furthermore, larvae fed on *A. kuehniella* eggs during their development and thereafter fed *A. pisum*, showed a reduced demand for aphids compared to larvae reared on aphids (Ettifouri and Ferran, 1993). This reduction in demand may result from the modification of the predator's ability to recognize visual and/or olfactory stimuli associated with aphids (Ferran et al., 1997).

For aphidophagous predators, the duration of larval instars as well as the reproductive capacity is influenced by the aphid species consumed. Kalushkov and Hodek (2004) noted that *C. septempunctata* showed twice as high fertility when fed with *A. pisum* and *Sitobion avenae* (Fabricius, 1775) than when fed on *Aphis fabae* and *Aphis craccivora* Koch, 1854.

Regarding the life table, the highest specific fertility was observed in individuals fed *C. atlantica*, demonstrating that the production of offspring per female during the lifetime of *H. axyridis* is optimized on this diet. The decrease in reproductive capacity of the predator with age is related to the decrease in the activity levels of coccinellids as they get older (Frechette et al., 2004). Dixon and Agarwala (2002) observed that the decrease in egg production and fertility with age of *H. axyridis* is associated with the decrease in walking speed and consumption and assimilation of aphids.

The results obtained in the life tables and for fertility showed that the three diets were similar for most indicators. According to Horm (1988), if R_o is greater than 1, the population is increasing, which was observed for the three diets evaluated. However, insects that fed *C. atlantica* showed the highest R_o value, which was statistically different from diet 3. Garcia (2002) stresses the importance of R_o to evaluate the quality of insect rearing, since generation time (T), which is also involved in the calculation of finite population increase (λ) and the intrinsic rate of increase (r_m) can be influenced by environmental variables, whereas R_o is an innate characteristic of the population.

The time interval between each generation observed by Santos et al. (2014) and Castro et al. (2011), using diet 1 as food was lower than that obtained in the present study. Also lower was the value found by Lanzoni et al. (2004), and also for the other two species, *H. variegata* and *A. bipunctata*, as well as when females were fed with fresh eggs compared to frozen eggs of *Sitotroga cerealella*, at 27 °C (Abdel-Salam and Abdel-Baky, 2001).

For r_m, a close value was obtained by Castro et al. (2011) using *C. atlantica* as food, unlike Santos et al. (2014), who obtained a higher value. At 25 °C, Lanzoni et al. (2004) found a far lower value than in this study, using *M. persicae* as food.

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

Van Lenteren (1986) states that a biological control agent is considered effective if its r_m values are similar or higher than that of its prey, which will favor the establishment of the natural enemy, and in this case, predator introductions should be regular. Therefore, *H. axyridis* has a good innate ability to increase in number, because r_m values were higher than most of the values observed for *C. atlantica*, and this may favor its establishment in certain places (Penteado, 2007; Castro et al., 2011).

This innate ability to increase in number can be considered a specific feature, although it is very strongly affected by environmental changes. In general, this parameter is better defined for a particular type of environment. When environmental conditions are favorable, the capacity of the population to increase in number is positive, and when it is unfavorable, this capacity is negative. The importance of this parameter is that it offers us a model with which to compare the rates obtained in the laboratory with those observed in nature, translating the biotic potential of the species. In natural, innate ability to grow will depend on the fertility, longevity and development speed of the species (Penteado, 2007).

This rate of population increase, according to Kiyindou and Fabres (1987), is very important to compare the performance of the species under different environmental conditions and of different species reared under similar conditions. Castro et al. (2011), also using diet 1, found a λ value greater than that in the present study, as well as that of Santos et al. (2014) and of Abdel-Salam and Abdel-Baky (2001) with females fed with fresh eggs *S. cerealella*, at 27 °C. The λ value reinforces the values obtained for R_o, revealing that there is a population increase from one generation to another (Penteado, 2007). However, several ecological factors, biotics and abiotics, such as predation, parasitism, temperature, light and climate can affect the growth of this species in the field, reducing the offspring. Ecological life tables can be used in the evaluation of performance under these conditions (Hodek et al., 2012).

According to these results and others in the literature, the type of food clearly influences the biological variables of *H. axyridis*. Also, even managing to survive and reproduce feeding on a non-aphid diet, the overall results of life and fertility tables, along with biological data, indicated that it performed better when feeding on these prey.

The large majority of species of Coccinellidae consume alternative food, such as pollen, sugar, yeast, fruit and plants, as an integral part of their diet. These aliments serve to increase energy and assist in migration, providing survival in periods of prey scarcity and improve reproductive capacity. However, the suitability of alternative food differs between coccinellid species (Lundgren, 2009).

The ability to use other food resources, when the preferred one is scarce, provides a competitive advantage to *H. axyridis* over other coccinellid predators that share the same niche, and are less able to exploit new food sources. This fact allows *H. axyridis* to develop and reproduce in harsh conditions and also to explore new habitats, thus increasing its coverage area.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

We thank Dr. Al Leyva who helped with the English translation of the manuscript. Heartfelt gratitude is also expressed to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Masters fellowship to the first author and for Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) fellowship to LMA (# 306772/2006-0).

References

Abdel-Salam, A.H., Abdel-Baky, N.F., 2001. Life table and biological studies of *Harmonia axyridis* Pallas (Col. Coccinellidae) reared on the grain moth eggs of *Sitotroga cerealella* Olivier (Lep., Gelechiidae). J. Appl. Entomol. 125, 455–462.
Ashaf, M., 2010. A study on laboratory rearing of lady bird beetle (*Coccinella septempunctata*) to observe its fecundity and longevity on natural and artificial diets. Int. J. Biol. 2, 165–173.
Berkvens, N., Bonte, J., Berkvens, D., Tirry, L., De Clercq, P., 2008. Influence of diet and photoperiod on development and reproduction of European populations of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). BioControl 53, 211–221.
Blackman, R.L., 1965. Studies on specificity in Coccinellidae. Ann. Appl. Biol. 56, 336–338.
Castro, C.F., Almeida, L.M., Penteado, S.R.C., 2011. The impact of temperature on biological aspects and life table of *Harmonia axyridis* (Pallas) (Coleoptera Coccinellidae). Fla. Entomol. 94, 923–932.
De Clercq, P., Bonte, M., Vanspeybroeck, K., Bolckmans, K., Anddeforce, K., 2005. Development and reproduction of *Adalia bipunctata* (Coleoptera Coccinellidae) on eggs of *Ephestia kuehniella* (Lepidoptera: Phycitidae) and pollen. Pest. Manag. Sci. 61, 1129–1132.
Dixon, A.F.G., 2000. Insect Predator–Prey Dynamics: Ladybird Beetles and Biological Control. Cambridge University Press, Cambridge.
Dixon, A.F.G., Agarwala, B.K., 2002. Triangular fecundity function and ageing in ladybird beetles. Ecol. Entomol. 27, 433–440.
Ettifouri, M., Ferran, A., 1993. Influence of larval rearing diet on the intensive searching behavior of *Harmonia axyridis* larvae. Entomophaga 38, 51–59.
Ferran, A., Gambier, J., Parent, S., Legendre, R., Tournière, R., Giuge, L., 1997. The effect of rearing the ladybird *Harmonia axyridis* on *Ephestia kuehniella* eggs on the response of its larvae to aphid tracks. J. Insect Behav. 10, 129–144.
Frechette, B., Dixon, A.F.G., Alauzet, C., Hemptinne, J-L., 2004. Age and experience influence patch assessment for oviposition by an insect predator. Ecol. Entomol. 29, 578–583.
Fox, J., 2003. Effect displays in R for generalised linear models. J. Stat. Softw. 8, 1–27.
Garcia, J.F., 2002. Técnica de criação e tabela de vida de Mahanarva fimbriolata (Stal, 1854) (Hemiptera: Cercopidae). Dissertação de mestrado. ESALQ/USP, Piracicaba, pp. 59.
Giorgi, J.A., Vandenberg, N.J., McHugh, J.V., Forrester, J.A., Ślipiński, A., Miller, K.B., Shapiro, L.R., Whiting, M.F., 2009. The evolution of food preferences in Coccinellidae. Biol. Control 51, 215–231.
Guedes, C.F.C., 2013. Preferência alimentar e estratégias de alimentação em Coccinellidae (Coleoptera). Oecol. Aust. 17, 59–80.
Guedes, C.F.C., Almeida, L.M., 2013. The potential of different fruit species as food for *Harmonia axyridis* (Pallas, 1773) (Coleoptera Coccinellidae). Rev. Bras. Frut. 35, 1025–1031.
Hamasaki, K., Matsui, M., 2006. Development and reproduction of an aphidophagous coccinellid, *Propylea japonica* (Thunberg) (Coleoptera Coccinellidae), reared on an alternative diet, *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. Appl. Entomol. Zool. 41, 233–237.
Hodek, I., 1973. Biology of Coccinellidae. Academia/Dr W. Junk, Prague/The Hague.
Hodek, I., Ruzicka, Z., Hodková, M., 1978. Pollinivorie et aphidophagie chez *Coleomegilla maculata* (DeGeer). Ann. Zool. Ecol. Anim. 10, 453–459.
Hodek, I., Honěk, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht.
Hodek, I., Van Emden, H.F., Honěk, A., 2012. Ecology of Coccinellidae. Wiley-Blackwell, Dordrecht.
Horm, D.J., 1988. Ecological approach to pest management. Guilford Press, New York.
Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363.
Jalali, M.A., Tirry, L., De Clercq, P., 2009. Effects of food and temperature on development, fecundity and life-table parameters of *Adalia bipunctata* (Coleoptera: Coccinellidae). J. Appl. Entomol. 133, 615–625.
Kalushkov, P., Hodek, I., 2004. The effects of thirteen species of aphids on some life history parameters of the ladybird *Coccinella septempunctata*. BioControl 49, 21–32.
Kiyindou, A., Fabres, G., 1987. Étude de la capacité d'accroissement chez Hyperaspis raynevali (Coleoptera: Coccinellidae) prédateur introduit au Congo pour la regulation des populations de *Phenacoccus manihoti* (Homoptera: Pseudococcidae). Entomophaga 32, 181–189.
Koch, R.L., 2003. The Multicolored Asian Lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control and non-target impacts. J. Insect Sci. 32, 1–16.
Koch, R.L., Venette, R.C., Hutchison, W.D., 2006. Invasions by *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) in the Western Hemisphere: Implications for South America. Neotrop. Entomol. 35, 421–434.
Lanzoni, A., Accinelli, G., Bazzocchi, G.G., Burgio, G., 2004. Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata* and *Adalia bipunctata* (Col. Coccinellidae). J. Appl. Entomol. 128, 298–306.
Lundgren, J.G., 2009. Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. Biol. Control 51, 294–305.
Lundgren, J.G., Wiedenmann, R.N., 2004. Nutritional suitability of corn pollen for the predator *Coleomegilla maculata* (Coleoptera: Coccinellidae). J. Insect Physiol. 150, 567–575.
Majerus, M.E.N., 1994. Ladybirds. Harper Collins, London.

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003

Martins, C.B.C., Almeida, L.M., Zonta-de-Carvalho, R.C., Castro, C.F., Pereira, R.A., 2009. Harmonia axyridis: a threat to Brazilian Coccinellide? Rev. Bras. Entomol. 53, 663–671.
Maurice, N., Pervez, A., Kumar, A., Ramteke, P.W., 2011. Duration of development and survival of larvae of *Coccinella transversalis* fed on essential and alternative foods. Eur. J. Environ. Sci. 1, 24–27.
McCornack, B.P., Koch, R.L., Andragsdale, D.W., 2007. A simple method for in-field sex determination of the multicolored Asian lady beetle *Harmonia axyridis*. J. Insect Sci. 7, 1536–2442.
Meyer, J.S., Igersoll, C.G., Macdonald, L.L., Boyce, M.S., 1986. Estimating uncertainty in population growth rates: jackknife vs bootstrap techniques. Ecology 67, 1156–1166.
Niijima, K., Abe, W., Matsuka, M., 1997. Development of low-cost and labor-saving artificial diet for mass production of an aphidophagous coccinellid, *Harmonia axyridis* (Pallas). Bull. Fac. Agric. 37, 63–74.
Omkar, Srivastra, S., 2003. Influence of six aphid prey species on development and reproduction of ladybird beetle, Coccinella septempunctata. Biol. Control 48, 379–393.
Osawa, N., 2000. Population field studies on the aphidophagous ladybird beetle *Harmonia axyridis* (Coleoptera: Coccinellidae): resource tracking and population characteristics. Popul. Ecol. 42, 115–127.
Penteado, S.R.C., 2007. *Cinara atlantica* (Wilson) (Hemiptera, Aphididae): um estudo de biologia e associações. Tese de doutorado. Universidade Federal do Paraná, Curitiba.
Penteado, S.R.C., Oliveira, E.B., Lazzari, S.M.N., 2010. TabVida - Sistema computacional para cálculo de parâmetros biológicos e de crescimento populacional de afídeos. Embrapa Florestas, 1 CD-ROM, Colombo (Embrapa Florestas. Documentos, 203).
Pervez, Omkar, A., 2004. Prey dependent life attributes of an aphidophagous ladybird beetle, *Propylea dissecta* (Mulsant). Biocontrol Sci. Technol. 14, 385–396.
Phoofolo, M.W., Obrycki, J.J., 1995. Comparative life history studies of Nearctic and Palearctic populations of *Coccinella septempunctata* (Coleoptera Coccinellidae). Environ. Entomol. 24, 581–587.
R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, Available at: http://www.R-project.org (accessed 04.08.13).
Santos, N.R.P., Santos-Cividanes, T.M., Cividanes, F.J., Anjos, A.C.R., Oliveira, L.V.L., 2009. Aspectos Biológicos de *Harmonia axyridis* alimentada com duas espécies de presas e predação intraguilda com *Eriopis connexa*. Pesqui. Agropecu. Bras. 44, 554–560.
Santos, A.A., Almeida, L.M., Castro-Guedes, C.F., Penteado, S.C.R., 2014. Life table analysis and consumption capacity for *Harmonia axyridis* (Coleoptera Coccinellidae), feeding on *Cinara atlantica* (Hemiptera: Aphididae). Fla. Entomol. 97, 1702–1709.
Soares, A.O., Coderre, D., Schanderl, H., 2001. Fitness of two phenotypes of *Harmonia axyridis* (Coleoptera Coccinellidae). Eur. J. Entomol. 98, 287–293.
Soares, A.O., Coderre, D., Schanderl, H., 2005. Influence of prey quality on the fitness of two phenotypes of *Harmonia axyridis* adults. Entomol. Exp. Appl. 114, 227–232.
Specty, O., Febvay, G., Grenier, S., Delobel, B., Piotte, C., Pageaux, J.F., Ferran, A., Guillaud, J., 2003. Nutritional plasticity of the predatory ladybeetle harmonia axyridis (Coleoptera Coccinellidae): comparison between natural and substitution prey. Arch. Insect Biochem. 52, 81–91.
Sutherland, A.M., Parrella, M.P., 2009. Mycophagy in Coccinellidae: review and synthesis. Biol. Control 51, 284–293.
Van Lenteren, J.C., 1986. Parasitoids in the greenhouse: successes with seasonal inoculativa release systems. In: Waage, J., Greathead, D. (Eds.), Insect parasitoids. Academic Press, London.
Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer, New York.

Please cite this article in press as: de Castro-Guedes, C.F., et al. Effect of different diets on biology, reproductive variables and life and fertility tables of *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae). Rev. Brasil. Entomol. (2016). http://dx.doi.org/10.1016/j.rbe.2016.03.003